

How might individual honeybees measure massive volumes?

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We suggest how individual honeybees might measure the large volumes of potential nest sites and propose a key experimental test for our model.

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1. A NEW ALGORITHM FOR VOLUME ESTIMATION

When honeybees swarm, individual bees need to measure the volume of potential nest cavities (Seeley 1977; Seeley & Buhrman 2001). These cavities are massive compared with the size of an individual honeybee. Preferred cavities have a volume of 40 l (Seeley & Buhrman 2001), and may need to accommodate 30 000 bees plus their honeycombs. How can an individual honeybee measure such large irregular volumes with reasonable accuracy?

It is known that individual honeybees invest much time walking the inner surface of a cavity and Seeley (1977) has hypothesized that they may even use 'a form of vector calculus' to estimate volume from such measurements. Here, we show that, in principle, honeybees could use a much simpler method.

Physicists have long known that for an ergodic volume (i.e. an omni-accessible three-dimensional space)

$$\text{MFPL} = 4V/A \quad (1.1)$$

(see the expression for mean chord length in Case & Zweifel (1967, p. 56)), where MFPL is mean free path length, V is volume and A is internal surface area.

So volume is proportional to mean free path length multiplied by internal surface area. Equation (1.1) has its origin in work that can be traced back to James Clerk Maxwell (1879) as cited in Joyce (1975).

Thus if a honeybee can estimate both the internal surface area and the mean free path length of a cavity, it may be able to estimate its volume. Because cavity selection mostly involves rejection of volumes that are too small (Seeley 1977), all the bee might need to do is to satisfy itself that a cavity provides a suitable combination of internal surface area and mean free path length.

2. MEASURING AREA

How might bees measure internal surface area? Recent work has shown that individual ants can estimate the floor area of potential nest sites. Mallon & Franks (2000) provide evidence that they use a Buffon's needle algorithm. Buffon, in the late eighteenth century, derived a method for estimating π empirically, by dropping a needle onto a

plane inscribed with parallel lines. If the distance between the lines is more than the length of the needle, the frequency of intersections between the repeatedly dropped needle and the lines can be used to estimate π . Buffon's formula can be rearranged to estimate area from the frequency of intersections of two sets of random lines. Mallon & Franks (2000) have shown that *Leptothorax* ants deploy individual specific trail pheromones when first visiting a potential nest site and on a later visit probably estimate their intersection frequency with such trails to estimate area.

Honeybees also explore the internal surface of potential nests. Seeley (1977) has shown through elegant experiments that honeybees can be fooled into accepting a new nest cavity that is too small if they are forced to walk unusually long distances within it. He did this by building a cylindrical potential nest cavity with an internal rotatable sleeve, which could be used to manipulate the bee's walking distance. This suggests that honeybees might not be using a Buffon's needle algorithm, because rotating the sleeve should not affect their path crossing frequency. However, they might simply use the distance they walk, say to return to the nest entrance, as a measure of area. Honeybees do not lay trail pheromones *per se*, but they do have tarsal glands that produce an oily exudate, the so-called 'footprint pheromone', that is deposited wherever a bee walks. This may be used to help bees recognize a hive entrance (Butler *et al.* 1969; Duffield *et al.* 1984). Seeley (1977) did not propose how such walking bees might estimate the surface area of potential cavities or indeed if they use surface area at all in their estimation of volume. However, it is likely that such walking can be used to measure area more easily than it can be used to measure volume without additional information.

3. MEASURING MEAN FREE PATH LENGTH

One key issue remains: how could honeybees estimate mean free path length? There are three possibilities. First, they might look across the cavity and estimate the distance to the nearest wall visually. Second, bees might conceivably use sound to judge the distance of the opposite wall or even the size of the volume. For example, Robert & Göpfert (2002) have recently suggested that flies might use echolocation to judge distance. However, the required sensory system has not been shown to exist in bees. Third, they might use short hopping flights inside the cavity to determine how far they can fly on average before hitting a wall. The experiments by Seeley (1977) suggest that honeybees can estimate nest volume in very low light intensities i.e. they do not need sight to estimate mean free path length. Seeley also notes that house-hunting bees use short hopping flights within nest cavities (see also Seeley 1982). Seeley (1977) made no suggestion that such short flights had any role in volume estimation. Indeed, he provided no explanation for the occurrence of such flights. However, it is noteworthy that these intra-cavity flights are short and direct (i.e. hops) rather than long and winding (Seeley 1977).

Here, we suggest that these short intra-cavity flights may be used to estimate mean free path lengths within the ergodic volume of potential nest cavities and this together with an estimate of the area of internal surface of a cavity might enable a bee to estimate volume.

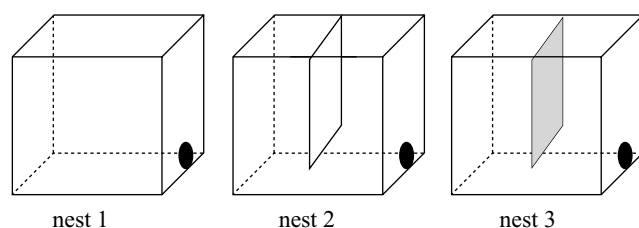


Figure 1. These nest-box designs could be used to test how honeybees measure volume. Nests 2 and 3 have a partial partition inserted into them, and in nest 3 this partition is coated with Fluon so bees cannot walk on it. All have the same volume; nest 3 has the same (walkable) surface area as nest 1, and the same mean free path length as nest 2.

4. SUGGESTED EXPERIMENTAL TEST

Our model could be tested by providing house-hunting honeybee swarms with choices among three potential nest sites (figure 1). The first would be a standard 40 l nest-box (see Seeley & Buhrman 2001). The second would be similar to the first, but would have a partial partition hanging from its roof. The third would be identical to the second but the partial partition would be painted with Fluon to prevent a bee walking over it. All nest-boxes have to be dark, such that bees cannot use visual cues. Our model predicts that the honeybees should not discriminate between nests 1 and 2 and should prefer either to nest 3. Why? Nest 2 should be just as acceptable as nest 1 because it will have (almost) the same volume. Furthermore, when a honeybee is assessing nest 2 its estimate of internal surface area should be greater than that for nest 1 and this should exactly compensate for a reduction in the mean free path length it measures. Nest 3 should be discriminated against because it will give a smaller mean free path length than nest 1 and a smaller surface area than nest

2 because bees will not be able to walk on the Fluon-painted partition.

Of course, we are not suggesting that a honeybee understands the statistical mechanics of James Clerk Maxwell any more than we are suggesting that ants understand Buffon's needle. But our application of classical formulae from physics and mathematics may suggest how evolution by natural selection has enabled social insects to use simple rules of thumb to solve seemingly very difficult problems.

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